Behavioral Adaptations of Cryptic Moths. II. Experimental Studies on Bark-like Species

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Abstract: Three experiments were conducted on a variety of bark-like geometrid and noctuid moths, using an experimental apparatus which allowed a choice between black and white backgrounds. These experiments indicated that the appropriate background selections of the moths studied in this apparatus were not the result of (1) simple photo-tactic escape responses, (2) "imprinting" processes occurring shortly after emergence, or (3) reflectance-matching mechanisms, involving comparisons of wing and background reflectances. These results are viewed as additional evidence for genetically fixed reflectance preferences in bark-like cryptic moths.

Prior studies have demonstrated that a variety of bark-like geometrids and noctuids will select appropriate backgrounds in an experimental apparatus which presents a choice of backgrounds differing in reflectance (Kettlewell, 1955; Sargent, 1966; Sargent and Keiper, 1969). In addition, by painting the circumocular scales of two species, and thereby altering their reflectances, I have obtained evidence which suggests that these background preferences are genetically fixed (Sargent, 1968).

The present paper summarizes results from three additional experiments which were carried out during the summer of 1968 in Leverett, Franklin Co., Massachusetts. The first of these experiments was designed to determine whether appropriate background selections of cryptic moths in an experimental apparatus might simply be due to photo-tactic escape responses (i.e. movement toward the lightest or darkest portions of the apparatus). The second experiment was an attempt to determine whether cryptic moths might "imprint" to particular backgrounds shortly after emergence, and subsequently select backgrounds of similar reflectance. Finally, the third experiment was designed to determine whether the wings (and flight) of cryptic moths are necessary for their selection of appropriate backgrounds.

GENERAL METHODS AND MATERIALS

The apparatus used in these experiments consisted of a plywood box (15 inches square by 19 inches high), into which a cylinder (44 inches in circumference and 19 inches high) was set. This cylinder was formed of four painted sections of blotting paper (each 11 by 19 inches), two black and two white.

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Phigalia titea

POSITION OF MOTHS	BACKGROUNDS Black	White
Upper Half	28	64
Lower Half	24	49

Fig. 1. The distribution of individuals of *Phigalia titea* on the black and white backgrounds, in both the upper and lower halves of the experimental apparatus.

These sections were arranged vertically in an alternating black and white sequence. The entire apparatus was covered with a pane of window glass, and placed in a wooded area where a thick canopy excluded direct sunlight. Moths were introduced into the cylinder by sliding the glass top to one side.

The moths were taken at 150-watt Westinghouse outdoor spotlights at my home in Leverett, Massachusetts. Immediately after capture, and any experimental manipulation, the moths were released into the experimental apparatus. The following morning, between 0600 and 0800 EST, the positions of the moths in the apparatus were noted.

THE EXPERIMENTS AND RESULTS

EXPERIMENT 1. It has been suggested that the tendencies of light moths to select light backgrounds, and dark moths to select dark backgrounds, in experimental situations might be the result of positive and negative photo-tactic escape responses respectively. If this were the case, one would expect light moths to come to rest near the top of the white backgrounds in my experimental apparatus (i.e. close to the light source), and dark moths to rest near the bottom of the black backgrounds. To test this possibility, I noted whether resting individuals of several species were in the upper or lower half of the experimental apparatus when checking their background selections in the morning.

Results obtained with *Phigalia titea* Cramer (Geometridae), a species represented by a particularly large sample, are presented in Fig. 1. Analyses of these data reveal that (1) the total numbers of moths resting in the upper and lower halves of the experimental apparatus are not significantly different (chi-square 2.18, P greater than 0.10), and (2) the distributions of the moths on the different backgrounds in the upper and lower halves of the apparatus are not significantly different (chi-square 0.03, P greater than 0.80), both distributions revealing a highly significant preference for the white backgrounds (chi-squares greater than 8, both P less than 0.01). Similar results have been obtained with smaller samples of several other species, including the dark noctuids *Catocala*

Catocala antinympha

PRIOR HISTORY OF MOTHS	TEST BACKGROUNDS Black	White
Wild-Caught	11	1
White Background	5	0

FIG. 2. The distributions of wild-caught and previously "imprinted" individuals of *Catocala antinympha* on the black and white backgrounds of the experimental apparatus.

antinympha Hübner and *Chytonix palliatricula* Guenée. In these latter species there were also slight, but insignificant, preferences for the upper half of the apparatus, and here the black backgrounds were preferred in both halves.

EXPERIMENT 2. The possibility that moths might acquire background reflectance preferences through imprinting-like processes occurring shortly after emergence (see e.g. Thorpe, 1963) has been pointed out to me by several people. This possibility, although remote in my view, does seem to warrant some consideration in monophagous or oligophagous species whose usual host-plants possess bark which is similar in reflectance characteristics to the moths' wings. Such a situation prevails with *Catocala antinympha* Hübner (Noctuidae). The usual host-plant of this extremely dark moth is sweet fern, *Comptonia peregrina* [L.] Coulter, a shrub (not a true fern) with very dark bark. *C. antinympha* normally pupates in dead leaves beneath this host-plant, and therefore might often crawl up sweet fern stems after emerging.

To test this possibility of "imprinting," an experiment with *C. antinympha* was carried out. A number of larvae were collected from local sweet fern and reared in breeding cages (Ward's 14W 7500) until pupation. The pupae were then placed in an apparatus which was identical to that used in experiment 1, except that the backgrounds were all white. When the moths emerged, they crawled up on these white backgrounds, and were allowed to rest there for at least one day (minimum of 24 hrs., maximum of 36 hrs.). These moths were then tested in the black and white experimental apparatus in the usual manner. Although the number of moths used in this experiment was small, they all selected black backgrounds (Fig. 2), revealing a preference which did not differ from that of wild-caught controls (Fisher exact probability test, P equals 0.70).

EXPERIMENT 3. In a previous study (Sargent, 1968), the reflectances of two species were altered by painting the scales around their eyes (head, thorax, and bases of forewings). The background selections of these treated moths did not differ from those of controls, a result which was interpreted as evidence for genetically fixed background preferences in these species. However, the possibility

Campaea perlata

MOTHS	BACKGROUNDS Black	White
Controls	1	11
Wings removed	1	14

Fig. 3. The distributions of experimental (cyanide and wing removal) and control (cyanide only) individuals of *Campaea perlata* on the black and white backgrounds of the experimental apparatus.

remained that the moths might be reflectance-matching the unpainted portions of their wings with the backgrounds (perhaps in flight, when the wings could be viewed by the moths). Accordingly, another simple experiment was carried out on one of these species. *Campaea perlata* Guenée (Geometridae).

Several individuals of *C. perlata* were rendered inactive in a cyanide jar as they were collected. When the flutterings of these moths ceased, most of their wings were removed by scissors, cutting as close to the body as possible (and always removing at least three-quarters of the wing surface area). Upon recovery from the effects of the cyanide, these moths could not fly, but could crawl onto vertical surfaces. These moths were then tested in the black and white experimental apparatus, and their performance was compared to that of controls which received the cyanide treatment only (Fig. 3). The distributions of moths in the two groups on the experimental backgrounds did not differ (Fisher exact probability test, P equals 0.51), both groups exhibiting a highly significant preference for the white backgrounds (chi-squares greater than 8, both P less than 0.01).

DISCUSSION

The experiments reported here provide additional evidence for the view that background selections of cryptic moths are determined, at least in part, by reflectance characteristics of the backgrounds, and that these selections are based on genetically fixed reflectance preferences.

The results of the first experiment suggested that background selections do not result from simple photo-tactic responses. This result was expected in view of my field observations on bark-like cryptic species. For example, *Catocala antinympha*, which is very dark, almost always rests on dark tree trunks (e.g. young white pine, *Pinus strobus* L.), but often in very exposed situations.

The second experiment indicated that a moth's early adult experience does not influence its subsequent choices of backgrounds. This result was again expected in view of field observations. A relevant example is provided by *Cosymbia pendulinaria* Guenée (Geometridae) which normally feeds and pupates on sweet fern, *Comptonia peregrina*. Although the bark of sweet fern is very dark, this moth is very light and prefers to rest on light trees such as gray birch, *Betula populifolia* Marsh. The possibility of larval "imprinting" to the bark of a host-plant was not investigated, although situations like that described for *C. pendulinaria* would argue against such an event.

Finally, the results of the third experiment failed to support the view that background selections result from a reflectance-matching process, involving the moths' wings. Thus, all of the experimental results obtained to date provide evidence for genetically fixed background preferences in bark-like cryptic moths.

Literature Cited

Kettlewell, H. B. D. 1955. Recognition of appropriate backgrounds by the pale and dark phases of lepidoptera. Nature, **175:** 943.

Sargent, T. D. 1966. Background selections of geometrid and noctuid moths. Science, **154:** 1674–1675.

———. 1968. Cryptic moths: effects on background selections of painting the circumocular scales. Science, **159:** 100–101.

——— and R. R. Keiper. 1969. Behavioral adaptations of cryptic moths. I. Preliminary studies on bark-like species. Jour. Lepid. Soc. (*in press*).

Thorpe, W. H. 1963. Learning and Instinct in Animals. 2nd ed. Harvard Univ. Press, Cambridge, Mass. 558 pp.